ART. 8. NOTES ON THE MYLAGAULID RODENT DENTITION

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(Plate 23)

Attempts to identify mylagaulid rodents make it apparent that in many past discussions or descriptions, authors have been extremely indefinite about the proper names to apply to the individual teeth. This is not surprising in view of the highly specialized and unusual nature of the mylagaulid dentition, but it is nevertheless extremely confusing to the uninitiated student who does not at first fully appreciate the reasons for such vagueness. Carnegie Museum fortunately has in its paleontological collection three excellent mylagaulid lower jaws which preserve parts of the milk dentition. The three specimens are: CM 742, holotype of *Mesogaulus pristinus* (Douglass); CM 843, holotype of *M. proximus* (Douglass); and CM 723, *Mesogaulus* sp. [*Mylagaulus* sp. of Douglass]. Since Douglass described *M. pristinus* and *M. proximus,* they have been removed from the genus *Mylagaulus* Cope and placed by Cook and Gregory (1941: 551) in the genus *Mesogaulus* Riggs.

Douglass' interpretation (1903: 186-191) of the dental formula and succession in these specimens was summarily rejected by Matthew (1924: 77) as being erroneous. The Carnegie Museum specimens were restudied and this paper will review the interpretations of Douglass and Matthew and record some of the writer's own observations. Unfortunately, only lower jaws were available for study, so evidence of upper dentitions was taken from the literature.

The original descriptions by Douglass of the Carnegie specimens proved to be essentially accurate, but the text and labeling of the figures contain *lapsi* which must be recognized. In the quotations following, changes to make his discussion clearer, more accurate, or consistent are indicated in brackets. In a general description of the three specimens, all found in the upper Miocene beds along the lower Madison River valley, Montana, Douglass (1903: 186-87) said:

> In one specimen (*M. pristinus*) [should read *M. proximus*] the erupting large premolar was apparently pushing out with its posterior portion a short-crowned, long-rooted tooth. Its anterior portion is replacing a tooth, only a portion of one root of which remains. In two other specimens [*M. pristinus* and *M.* sp.] the large premolar has missed this short-crowned, rooted tooth; or the anterior portion of the latter has apparently been

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absorbed and its posterior portion still remains between the large premolar and first prismatic molar.

There can be little doubt that this last rooted tooth is a *milk molar.* It is not at all prismatic, has long roots, is much worn in the young animal, and in one case is being shed. The permanent premolar and the two permanent molars are prismatic. In the descriptions which follow, the rooted tooth above described will be designated as the fourth temporary molar, $dm_{\bar{4}}$ [$dP_{\bar{4}}$]. If the above conclusions be true the large, permanent, prismatic premolar replaces two temporary molars. In one specimen [*M. proximus*] the posterior inner root of $dm_{\bar{3}}$ [$dP_{\bar{3}}$] is still preserved in place. . . .

The molar that is wanting in the adult animal is apparently the first, as there is no evidence of the loss of $M_{\bar{3}}$. The development of the first molar is evidently prevented by the large, permanent premolar. Perhaps under favorable conditions rudiments of $M_{\bar{1}}$ might be found.

Describing the holotype of *M. pristinus* Douglass (1903:187-88) said:

Permanent premolar large, very high, and with short roots. The fourth temporary molar [$dP_{\bar{4}}$], which is retained in the present specimen, is short, low and has long roots. Molars $_{\bar{2}}$ and $_{\bar{3}}$ are of moderate size and hypsodont.

. . . .

$M_{\bar{2}}$ [$dP_{\bar{4}}$] is nearly worn out. It is closely crowded against the premolar, and on the anterior portion next to this tooth the enamel is absent. Like the corresponding tooth in specimen no. 723, to be described later, it looks as if the anterior portion of the tooth has been absorbed. If the animal had lived the tooth would evidently soon have been shed. $M_{\bar{2}}$ is prismatic and quite high though its lower portion cannot be seen. $M_{\bar{3}}$ cannot be very high on account of its proximity to the posterior portion of the incisor. It is undoubtedly much like the corresponding tooth of no. 723.

Describing the holotype of *M. proximus,* Douglass (1903: 189-90) said:

When the animal died the large permanent premolar was erupting and had nearly reached the alveolar border. This tooth, being much larger than its two predecessors [$dP_{\bar{3}-\bar{4}}$], the portion of the jaw containing the roots of the latter had to be absorbed. A small part of this alveolar portion, with one root of the anterior temporary molar [$dP_{\bar{3}}$] remains above the postero-external portion of the large premolar. The last temporary molar being unreduced in antero-posterior diameter was being pushed out by this new tooth. This last temporary molar has a larger grinding surface than that of *M. proximus,* but is low, nearly worn out, and has two long slender roots.

$P_{\bar{4}}$ is not as large, but it would undoubtedly have become larger as there is considerable space between its posterior border and the anterior border of $M_{\bar{2}}$. This last tooth is long vertically on account of its greater age,

longer than the premolar. It appears to be open below and not to have completed its growth. It is very doubtful if this tooth would be shed during the lifetime of the animal. It had not yet come into use, at least it is not worn, though it projects some distance above the alveolar border. $M_{\bar{3}}$ was just erupting.

Describing Carnegie Museum specimen no. 723 which he identified as *Mylagaulus* sp., Douglass (1903: 190) said:

The last temporary premolar is much reduced, as if by partial absorption, as in the specimen of *M. proximus* (no. 842). Its antero-posterior is half its transverse diameter. The crown is nearly worn down to the roots. $M_{\bar{2}}$ is not so high as in *M. pristinus*. $M_{\bar{3}}$ is still lower. Both molars might be shed in old age.

From the above quotations and his figures, the concept Douglass had concerning the identities of the teeth in the three specimens is clear. He thought the large, hypsodont premolar was $P_{\bar{4}}$ and believed the two low-crowned, long-rooted teeth that it replaced were $dP_{\bar{3}}$ and $dP_{\bar{4}}$. He considered the last two teeth to be $M_{\bar{2}}$ and $M_{\bar{3}}$. (On figure 28 of Douglass' paper the last molar is mislabeled. From his discussion he must have meant to label that tooth $M_{\bar{3}}$? instead of $M_{\bar{1}}$?)

Matthew (1924: 77) remarked:

The molars in the mylagaulidae are progressively deciduous, $M_{\bar{1}}$ dropping out shortly after the large premolar breaks through the jaw, $M_{\bar{2}}$ and $M_{\bar{3}}$ at later stages of wear. The alveolus of $M_{\bar{1}}$ is early reduced and disappears as the premolar pushes its way upward; the alveolus of $M_{\bar{2}}$ is similarly eliminated and that of $M_{\bar{3}}$ is reduced and finally disappears before the premolar is wholly worn down. Mr. Douglass [1903] has interpreted the $M_{\bar{1}}$ as $dP_{\bar{4}}$ and the $P_{\bar{4}}$ as $P_{\bar{3}}$, but this interpretation is certainly erroneous.

Discussing the mylagaulid dentition (1924: 81) Matthew said:

A lower jaw obtained in 1921 gives the long desired evidence of the milk dentition in this group. . . . The milk premolar is a short-crowned *Allomys*-like tooth, totally unlike its permanent successor.

The jaw referred to by Matthew, A.M.N.H. 18902, was identified and figured by him (1924, fig. 8) as *Mylagaulus vetus*. This species later was assigned to the genus *Mesogaulus* by Cook and Gregory (1941:551).

My examination of the Carnegie specimens leads me to suspect that neither Douglass nor Matthew was completely correct in this matter, but that Douglass was more nearly so. Both authors and subsequent writers seem agreed to call the large, hypsodont permanent premolar

$P_{\bar{4}}$. The only apparent objection to this lies in the fact that this tooth rises beneath two deciduous teeth, both of which appear to belong to the milk dentition and which I believe to be $dP_{\bar{3}}$ and $dP_{\bar{4}}$. In early stages its crown lies mostly below $dP_{\bar{3}}$, but its base lies partly below $dP_{\bar{4}}$ and shortly after eruption the crown would fill the space previously occupied by both teeth. It seems best to refer to this last premolar as $P_{\bar{4}}$ rather than to suppose that it is $P_{\bar{3}}$ with $P_{\bar{4}}$ missing.

Between the large permanent premolar and the hypsodont molar behind it lies a tooth whose identity is in dispute. Douglass called it $dP_{\bar{4}}$ and Matthew called it permanent $M_{\bar{1}}$. Matthew apparently based his decision upon the condition in the previously mentioned lower jaw of *M. vetus,* where the permanent premolar appears to be rising wholly beneath a rather similar deciduous tooth which is anterior-most in a series of four teeth. His assumption was that $P_{\bar{4}}$ replaced $dP_{\bar{4}}$. I recently failed to locate the jaw or any record of its whereabouts at the American Museum. One cannot tell for certain from Matthew's figure whether or not the second tooth in the premolar-molar series is brachyodont or hypsodont. The amount of wear on the second tooth appears too great even for an early erupting M_1 and seems to relate it more closely to the preceding deciduous premolar. The side view of the tooth suggests that it may be brachyodont. So, it is possible that the two anterior teeth in the A.M.N.H. specimen (no. 18902) of *M. vetus* are both deciduous. In the Carnegie Museum specimens, the nature of the last brachyodont, double-rooted tooth suggests that it is a deciduous premolar, $dP_{\bar{4}}$, as Douglass maintained rather than permanent $M_{\bar{1}}$ as considered by Matthew. The evidence for this belief, most of which has already been stated by Douglass and quoted here, is as follows:

1. The tooth is brachyodont, while the molar teeth behind and the permanent premolar in front are hypsodont. Unless the tooth was under separate genetic control, which is improbable, instead of belonging to the same genetic field as the other permanent teeth, it is difficult to suppose that as $M_{\bar{1}}$ (instead of $dP_{\bar{4}}$) it would remain brachyodont in the midst of a strongly hypsodont dentition.
2. It possesses two long roots while the permanent teeth behind are single-rooted.

3. The roots are not the secondary result of partial resorption due to crowding by the large premolar, because the enamel, which extends the full length of the hypsodont teeth, does not extend down the roots of this tooth but is restricted to the low crown. Also, there is considerable space in CM 843 between the large premolar and hypsodont molar, so that neither tooth is crowding the roots of the tooth between.

4. In the holotype of *M. proximus* this tooth is actually being pushed up and out by the hypsodont premolar and molar.

5. In degree of wear and nature of its roots, it closely resembles the deciduous molar in *M. vetus* and *M. novellus* Matthew (1924: 84) that Matthew called $dP_{\bar{4}}$. It bears no resemblance to the hypsodont permanent premolar and molars. This is the same condition which Matthew (1924: 81), as quoted above, considered to be indicative of the deciduous nature of the tooth being replaced by $P_{\bar{4}}$ in *M. vetus*. Matthew proposed that the last brachyodont, long-rooted tooth in the Carnegie specimens was $M_{\bar{1}}$. This would require that $M_{\bar{1}}$ erupted as part of the premolar series, was worn out and nearly lost before the permanent teeth came into wear.

The evidence then is taken as strongly favoring the original interpretation of Douglass that this tooth is $dP_{\bar{4}}$.

White (1952: 199-200) stresses the fact that the activity of the thyroid strongly influences the nature of teeth by its effect on metabolism and growth. He further cites the inhibitory effect which gonadic and adrenal cortex hormones have, beginning shortly before puberty, upon the growth stimulating effect of the thyroid. For an example of possible change in thyroid activity, he refers to the advanced form of milk dentition over permanent dentition in some late Tertiary horses and the advanced nature of $P_{\bar{3}}$ over $P_{\bar{4}}$ in *Hyracotherium*. On similar grounds, changed thyroid control might explain the seeming anomaly of a brachyodont $M_{\bar{1}}$ in the midst of a hypsodont permanent mylagaulid dentition. For instance, assume that the last long-rooted cheek tooth in mylagaulids is $M_{\bar{1}}$ and that the order of tooth germ formation and growth of the teeth was $dP_{\bar{4}}$-$M_{\bar{1}}$-$P_{\bar{4}}$-$M_{\bar{2}}$-$_{\bar{3}}$. Then, it is conceivable that a change in thyroid activity between the time of formation of $M_{\bar{1}}$ and $P_{\bar{4}}$ might result in an $M_{\bar{1}}$ which was distinctly different from the other

permanent teeth. However, in order for $M_{\bar{1}}$ to be brachyodont we would then have to conclude that thyroid activity, as affecting tooth growth, was increased rather than inhibited after the formation of $M_{\bar{1}}$. This would be exactly the reverse of what may have happened in White's examples of horses. Furthermore, the order of tooth formation was probably different, $M_{\bar{1}}$ forming after $P_{\bar{4}}$. A change in endocrine control of growth may in some manner be involved in the observable difference between low and high-crowned teeth. But, too many assumptions are necessary to support such a completely unusual situation. A much simpler and more normal interpretation, acceptable on similar grounds, would be that the last brachyodont tooth is $dP_{\bar{4}}$.

Both Douglass and Matthew regarded the last two molars as being $M_{\bar{2}}$ and $M_{\bar{3}}$. Douglass thought that $M_{\bar{1}}$ was missing completely, Matthew that it was the brachyodont tooth just discussed, and that it was lost early in the life of the animal. Douglass' quoted statement that there is no evidence for the loss of $M_{\bar{3}}$ is not necessarily correct. In the holotype of the early Miocene *Promylagaulus riggsi* McGrew, the upper dentition as McGrew figured it (1941, fig. 1) shows definite reduction of $M_{\bar{3}}$. Figure 3 of the same paper shows $M_{\bar{1}\text{-}\bar{3}}$ of a specimen identified by McGrew as *Promylagaulus* cf. *riggsi* in which $M_{\bar{3}}$ is apparently reduced. Although the tooth has just erupted, the dimensions of the triturating surface would not have increased much, if any, with wear. The hypsodont molars in the Carnegie specimens have been dissected to the base of their roots and show a decrease in diameter toward the base. The preceding two teeth in *Promylagaulus riggsi* appear from the figures to be at least somewhat hypsodont and thus to be molars. Furthermore, in five mylagaulid lower jaws in the Carnegie collection, all referable to *Mesogaulus,* the last of the two hypsodont molars was inclined forward in the jaw at an angle of 35-45 degrees from the teeth anterior to it. The specimens in which this can be seen are the three already listed, from Madison Valley, Montana plus CM 9565 from southeast of Fort Logan, Montana, and CM 8865 from the vicinity of Bozeman, Montana. This last molar also has a shorter root and impinges upon the posterior portion of the long, curved incisor which rises into the coronoid process. No space remains between the inclined molar, the incisor, and the dental foramen for another tooth. It therefore seems probable that reduction had occurred and was continuing posteriorly. Thus, $M_{\bar{3}}$ could have been eliminated at the stage

in the evolution of the mylagaulid lower dentition represented by the Carnegie specimens.

Johnson (1952) recorded evidence suggesting that upper and lower M3 have been lost in other rodents when he described the presence of an additional molar tooth in a specimen of *Mesembriomys* and reviewed similar occurrences of extra molar teeth in *Saccostomus, Microtus, Hystrix* and *Proechimys*. As he put it (p. 71), this supports the interpretation of others, whom he cites when he says that:

> Among rodents the anterior tooth in the series is homologous with the fourth deciduous premolar of other mammals (but not with the permanent premolar that usually replaces it), and that the remaining two teeth correspond to the first and second molars. If this is true, an occasional vestige of the lost third molar might be expected to appear at the posterior end of the tooth row.

Whether or not such a conclusion will ultimately prove applicable to all rodents, the embryological mode of tooth formation theoretically makes the loss of $M_{\bar{3}}$ much more likely than loss of $M_{\bar{1}}$ in any case. The permanent molar teeth arise in the embryo from the backward-growing, free extension of the dental lamina (Arey, 1941: 193). Any limitation of the continued backward growth of the dental lamina, such as the presence of the posterior portion of the long incisor in mylagaulids, might well interfere with the development of a full dentition at the posterior end of the molar series. On the other hand, interference with the growth of the dental lamina or the formation of tooth buds at the site of $M_{\bar{1}}$ might arrest development of all teeth posterior to it.

Matthew's statement (quoted) that the molars are deciduous progressively backward, does not receive support from study of CM 8865. In this specimen, which lacks the tooth crowns, the root division of $P_{\bar{4}}$ has approached to within less than three millimeters of the lip of the alveolus, yet both $M_{\bar{1}\text{-}\bar{3}}$ remained. It appears likely that $M_{\bar{1}}$ would have persisted as long as either $P_{\bar{4}}$ or $M_{\bar{3}}$. Certainly, in this specimen a long time would have separated the loss of $dP_{\bar{4}}$ ($M_{\bar{1}}$ of Matthew) and the loss of any of the permanent teeth.

SUMMARY AND CONCLUSIONS

Several lower jaws of *Mesogaulus* in the Carnegie Museum collection preserve parts of the milk dentition. Study of these leads to the

rejection in part of the interpretations of both Douglass and Matthew, concerning the identity of the lower teeth in these specimens. It is concluded that in mylagaulids, at least in those of the *Mesogaulus* stage, the enlarged, hypsodont $P_{\bar{4}}$ replaces two brachyodont, double-rooted deciduous premolars $dP_{\bar{3}}$ and $dP_{\bar{4}}$. The two hypsodont, single-rooted teeth behind are $M_{\bar{1}\text{-}\bar{2}}$. Deciduous upper dentitions were not available for study but Matthew's figures (1924, figs. 2, 5, 7) of *Mylagaulus laevis* Matthew and *M. vetus* suggest that similar conclusions may be applicable to the upper dentition.

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EXPLANATION OF PLATE 23

Comparison of lower teeth in three specimens of *Mesogaulus* from late Miocene beds along the Madison River, Montana. All figures ca. × 3/2

FIGS. 1, 2 *Mesogaulus proximus* (Douglass), holotype, CM 843, occlusal and lingual views, from photograph of original drawings published by Douglass (1903, fig. 27). Lower outlines of $M_{\bar{1}\text{-}\bar{2}}$ added as shown by dissection.

FIGS. 3, 4 *Mesogaulus* sp., CM 723, occlusal and labial views, from photograph of text figure, Douglass (1903, fig. 28).

FIGS. 5-7 *Mesogaulus pristinus* (Douglass), holotype, CM 742, occlusal, sectioned $P_{\bar{4}}$ and labial views, photographically *reversed* from original drawings published by Douglass (1903, fig. 26). Outline of $M_{\bar{2}}$ added as shown by dissection.